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POSTURAL REACTIONS OF INSECT ANTENNAE

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I

A bee held in a fixed position can respond to a motion of a visual pattern made up of stripes of equal width which is moved sidewise. The response is a definite movement of the antennae. The antennae assume with the onset of the shift of the pattern a definite position which is kept as long as the motion of the pattern continues; with cessation of the stripe motion the antennae move freely and independently. If, for instance, the pattern be moved from left to right, the left antenna will point at an angle of 90° to the bee's axis while the right antenna points straight forward. On reversing the motion of the pattern, the antennae take the reverse position (Wolf and Zerrahn-Wolf, 1935).

From earlier tests of visual acuity (Hecht and Wolf, 1929), intensity discrimination (Wolf, 1933*a* and *b*) and flicker (Wolf, 1933*c*) with freely creeping bees, it is known that a bee responds to a sudden displacement of a striped pattern which is moved underneath its creeping compartment, by a change of its course in a direction *against* the stripe motion. It therefore seems likely that the posture of the antennae recognizable with the bee held in a fixed position while viewing the moving stripes, is an expression of the bee's tendency to adjust its body posture in relation to the visual stimulus—just as a freely moving bee does by its turn against the stripe motion.

Postural responses of the antennae like those evidenced on stimulation by movement of a visual pattern can also be recognized under stimulation by gravity and centrifugal force.

II

If a bee is mounted in a small glass tube in such a way that the head sticks through a thin rubber membrane stretched across the end of the tube, while the thorax and abdomen are within the tube, the animal can easily be exposed to gravitational and centrifugal stimulation and the

postures of the antennae observed. The head end of the tube can be enclosed in a larger glass vessel so as to avoid the influence of gross air currents during motion, while the open abdominal end provides ample air for respiration. If properly fed, bees can be kept mounted in this way for days, and may be used repeatedly for experimentation. All responses described here are observed under conditions avoiding visual stimulation.

Vertical movements: If the animal is being lifted upward rapidly, both antennae swing upward and are kept rigid in this position until the movement ceases; thereafter the antennae move freely without any particular coördination of motion being noticeable (Fig. 1, *A*). During a downward movement both antennae are bent at a sharp angle, at the joint between the base and the flagellum, the tips of the antennae pointing almost straight downward (Fig. 1, *B*). During this motion both antennae also stay rigid and begin to move freely again when the downward motion ends. In repeating the up or down motion the antennae take their respective positions with great precision.

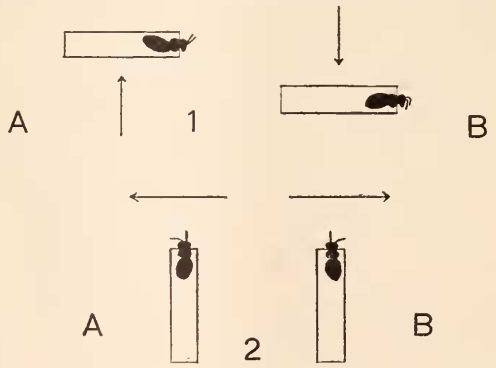

Fig. 1. Postures of the antennae of a bee held in a glass tube, when suddenly lifted vertically upward (*A*), and (*B*) when giving it a sudden downward motion.
Fig. 2. Postures of the antennae of a bee (seen from above) when moved horizontally with a motion perpendicular to the bee's body axis. Motion to the left (*A*) and to the right (*B*).

Horizontal movements: When moving a bee enclosed in a glass tube horizontally so that the direction of motion is perpendicular to the body axis, the antennae take definite position in relation to the direction of motion. The leading antenna (left antenna, while moving to the left) points at an angle of 90° to the body axis, whereas the following antenna points straight forward (Fig. 2, *A*). On reversing the direction of motion the antennae take reverse positions, the right antenna being bent at 90° to the body axis and the left antenna extended straight (Fig. 2,

B). That the antennae postures are not conditioned by visual stimuli is easily shown by the fact that the typical postures are induced by moving the bee against a uniform white background, or by making the tests in a darkroom with only a dim red light illuminating the bee.

If the bee is moved horizontally around in a large circle ($r = 1$ m.) the antenna toward the centre of the circle is bent at almost an angle of 90° while the outer antenna is extended straight (Fig. 3). Movements

FIG. 3. Postures of the antennae of a bee (seen from above) when moved horizontally on a circular course, facing in the direction of motion.

in the line of the bee's axis, however, do not elicit any definite position of the antennae; both can be held rigid at an angle of about 45° to the body axis or move freely and independently. The same holds for rectilinear vertical motion while the bee is facing straight upward or downward.

III

For the study of postural responses of the antennae of the bee under centrifugal force the following procedure was used (Fig. 4). On a turntable of 42 cm. diameter two right-angle prisms are mounted, one in the centre of the disc and the other close to the periphery. Underneath the turntable directly below the peripheral prism is a flashlight. Through an Eastman filter No. 91 the light illuminates an insect mounted in its glass enclosure and held by clamps in radial position on the turntable. Through the prism at the centre of the disc the bee's head is observed against the dark red background. By using a telescope above the central prism, focused on the bee's head, every motion and change in position of the antennae can easily be observed.

When a bee is placed in the holder with the turntable in *horizontal* position, and is facing radially toward the periphery of the turntable, typical postural responses of the antennae appear as the disc is slowly rotated through an angle of about 90° per second. The antenna of the side of the body in the direction in which the disc is turned points at an angle of 90° to the axis of the bee, while the other antenna points straight forward (Fig. 5). This position is held as long as the disc is in motion. On stopping, temporary compensatory movements of the antennae into reverse positions can be observed. When the bee in its tube is held so that its head points toward the centre of the disc, the same

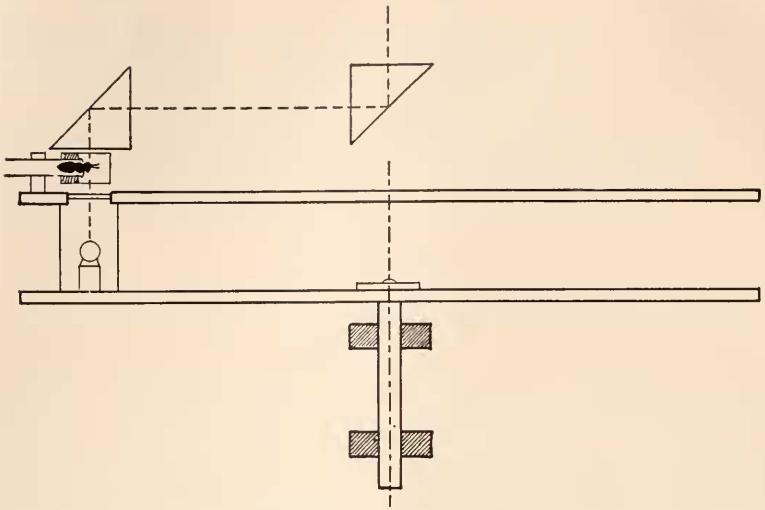

FIG. 4. Turntable for observation of postural responses of the antennae of the bee under the influence of centrifugal force; diagrammatic vertical section, through the axis of rotation, the holder for the insect, and the optical system.

antennal postures are noticed during rotation, i.e., the leading antenna bends at an angle of 90°, while the other antenna is straight.

With the turntable placed *vertically* the antennal postures show a dependence upon the bee's spatial position. A bee facing toward the centre of the disc while moving down will point downward with the leading an-

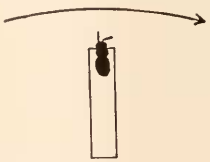

FIG. 5. Postures of the antennae of a bee during rotation when placed on a horizontal turntable facing radially toward the periphery.

tenna, while the other is straight. On arriving at the lowest point of the vertical circular course, both antennae are fully extended, almost parallel and straight. When moving upward again the leading antenna bends and reaches an angle of 90° to the body axis when the bee's axis has reached the horizontal. On moving further up so that in the extreme case the bee faces down vertically, both antennae are bent and retracted close to the head (Fig. 6, *A*). Passing the topmost point and then bringing the bee into the position from which the rotation was started, the original position of the antennae is again taken. When the bee is

facing toward the periphery of the turntable the leading antenna again points at an angle of 90° to the body axis and the other is straight, while the animal is either on its way downward or upward; whereas at the lowest point of the course both antennae are flexed and at the highest point both are fully extended (Fig. 6, *B*).

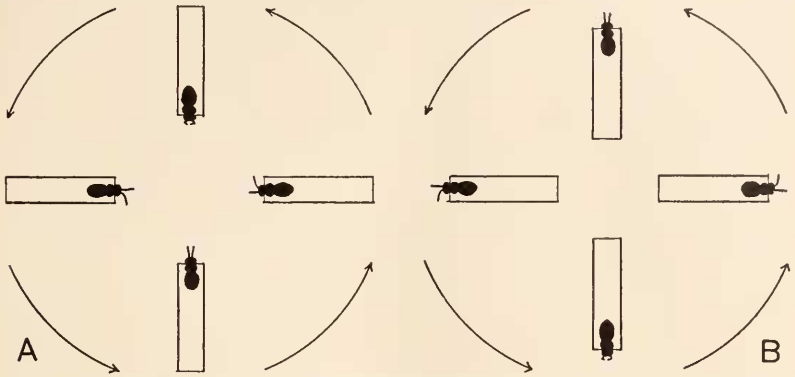

Fig. 6. Postures of the antennae of a bee during rotation on a turntable in vertical position: facing toward the center of the turntable (*A*), and toward the periphery (*B*).

Postural responses of the antennae are also exhibited when a bee in vertical position is rotated around its long body axis. The leading antenna points straight toward the side of the animal or is extended forward in the direction of rotation, whereas the following antenna is extended straight upward or is bent at the joint between base and flagellum, the tip then pointing also in the direction of rotation.

IV

On a turntable a free moving bee creeps generally against the direction of rotation, in a roughly circular course, if no visual stimuli are involved. The diameter of the bee's circular path depends upon the velocity of rotation, the diameter varying inversely with the speed of rotation. On a light background with dim red illumination the position of the bee's antennae can be followed in the darkroom. While the bee is moving freely—and when placed on the turntable it is almost continuously in motion—both antennae point at about an angle of 45° to the axis of the body. Only in case the bee has been resting in such a position that it faces radially toward the periphery or toward the centre of the turntable, can sudden motions of the antennae be noticed when the disc is set into rotation. As in the case when the bee is held in a fixed position, the antenna pointing in the direction of rotation swings out to

an angle of 90° to the body axis, while the other antenna points straight forward. The rotation, however, at once initiates circus movements of the bee; thus the bee starts its circular course and both antennae take positions at an angle of about 45° to the body axis. It has to be assumed that if the initial course of the bee, at the moment when the rotation begins, runs in the direction of the antenna which points at an angle of 90°, the bee's motion *against* the rotation of the turntable can only occur when the bee is facing toward the centre of the turntable; whereas a movement *with* the rotation should occur when the bee is facing toward the periphery. That this is the case can easily be demonstrated by waiting for a moment when the bee is moving radially toward the periphery of the turntable before starting the rotation. The bee under these conditions swings in a path in the direction of rotation of the disc, but as soon as the bee has described a quarter of a circle the animal's position becomes such that the leading rôle of the antenna which initiated the turn in that direction is taken over by the other one; consequently the bee describes a circular motion to the opposite side and now describes a course *against* the rotation of the disc. When the motion of the bee is not too fast, the shift in position of the antennae can be observed. It should be stated, however, that since the animal has to be kept underneath a glass cover and since, furthermore, its position is only rarely truly radial the picture is easily obscured. Stereotactic responses and unbalanced onset of excitation can lead to an initial turning *against* the rotation or can through contact with the wall of the container prolong the course *with* the rotation.

V

In all the cases described thus far, attention was paid only to the postures of the antennae. With the bee sealed in a tube, the only freely movable appendages are the antennae. Leg movements, leg postures, and the posture of the abdomen are hardly recognizable since the legs and the abdomen are or can be in close contact with the wall of the glass tube in which the bee is held. There are, however, indications that the abdomen takes definite postures as a result of gravitational and other mechanical stimulation.

If a bee is resting on its legs, a slight pressure on one side of the abdomen will initiate at once a bending of the antenna to the side where the pressure is applied, whereas the other one is extended straight forward. On releasing the pressure the abdomen swings to the side from which the pressure came. The same is true in case of applying an air current from one side. If under such conditions the bee turns around its centre, it always tends to move in a small circle into such a position

that it faces the air current. These responses are comparable to the homostrophic responses described in *Tenebrio* larvae (Crozier, 1924) and diplopods (Crozier and Moore, 1923).

Abdominal posture change is more clearly evident when during applied vertical motion the bee is held by the back of the thorax while the legs and the abdomen can be moved freely. During an upward motion the abdomen is then held straight or slightly bent upward at its tip, while during a downward motion it is strongly curved downward (as indicated in Fig. 1). Even during motions perpendicular to the bee's body axis while held in a tube, bending of the abdomen can be observed (Figs. 2 and 5), but these postural changes are never as clear and persistent as during suspension from the notum.

The definiteness of postural responses as indicated by the antennae may suggest that the antennae bear sense organs which are particularly susceptible to gravitational and centrifugal stimulation and thus are originators for postural reflexes. Thus it might be assumed that with the removal of the antennae the typical responses of an insect walking freely on a turntable might cease, or the postures of the abdomen might not be exhibited, when the animal is held fixed. No evidence to this effect could, however, be found. The typical responses persist after the antennae have been removed. There is no indication that the velocity of response or its extent is affected. At the same time the responses of the antennae are not affected when the abdomen is cut off. From recent work on proprioceptors in insects (Barnes, 1931; Pringle, 1938*a*, *b*, *c*), it is evident, however, that receptors responsible for postural reflexes are numerous and widely distributed over all parts of the insect's body, hence the mere removal of the antennae need not obliterate postural responses. On the other hand, there is strong evidence that the precision of orientation of the bee in its environmental field does involve functions of the antennae (Bethe, 1898, 1902; Wolf, 1926, 1927, 1930, 1931; Kalmus, 1937). Hence it can perhaps still be assumed that in the bee with antennae intact these organs play a part in the general exhibition of postural reflexes.

VI

In extending the observations on the bee, we also studied a series of other insects in respect to their antennal responses under gravitational and centrifugal force. In general, as far as a technical duplication of the tests was possible, the same reactions were found in several species of ants (*Formica, Lasius, Camponotus*) and in wasps (*Vespa maculata*). Among Coleoptera *Palidonota punctata* (*Scarabaeidae*) and *Pseudolucanus capriolus* (*Lucanidae*) gave clear antennal responses to rotation

and to sidewise translation. In other *Scarabaeidae,* such as *Macrodactylus subspinosus,* no reactions were noticeable. *Chlaenious sericeus* (*Carabidae*) did not show any response. Among butterflies we have so far tested only *Pieris rapae* (*Papilionidae*); no response could be noticed. *Blattidae,* particularly *Cryptocercus punctulatus* (Sudder), show very nice responses if the animal is prevented from keeping its antennae in contact with any solid object. The question might be raised whether the appearance of definite postural responses of the antennae is in some way related to the insect's ordinary habits in general, or to its velocity of progression in flight or in walking. Such questions, however, could only be answered after a systematic study of many insects.

Summary

Bees respond to gravitational and centrifugal stimulation by characteristic movements and postures of their antennae. Depending upon the direction of motion in relation to the bee's body, one or both antennae point against the direction of movement. Together with the antennal postures, definite postures of the abdomen can be observed. Free running bees also exhibit postural responses of the antennae which are correlated with the direction of progression under the influence of centrifugal force. Removal of the antennae does not eliminate postural responses of the body. In several other insects similar postural responses can be observed, while in certain forms they do not appear.

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